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Light and propagule pressure affect invasion intensity of *Prunus serotina* in a 14-tree species forest common garden experiment

Andrzej M. Jagodziński[1,2], Marcin K. Dyderski[1], Paweł Horodecki[1], Kathleen S. Knight[3], Katarzyna Rawlik[1], Janusz Szmyt[4]

1 *Institute of Dendrology, Polish Academy of Sciences, Parkowa 5, 62-035 Kórnik, Poland* **2** *Poznań University of Life Sciences, Faculty of Forestry, Department of Game Management and Forest Protection, Wojska Polskiego 71c, 60-625 Poznań, Poland* **3** *USDA Forest Service, Northern Research Station, 359 Main Road, Delaware, OH 43015, USA* **4** *Poznań University of Life Sciences, Faculty of Forestry, Department of Silviculture, Wojska Polskiego 69, 60-625 Poznań, Poland*

Corresponding author: *Andrzej M. Jagodziński* (amj@man.poznan.pl)

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Abstract

Experiments testing multiple factors that affect the rate of invasions in forests are scarce. We aimed to assess how the biomass of invasive *Prunus serotina* changed over eight years and how this change was affected by light availability, tree stand growth, and propagule pressure. The study was conducted in Siemianice Experimental Forest (W Poland), a common garden forest experiment with 14 tree species. We investigated aboveground biomass and density of *P. serotina* within 53 experimental plots with initial measurements in 2005 and repeated in 2013. We also measured light availability and distance from seed sources. We used generalized additive models to assess the impact of particular predictors on *P. serotina* biomass in 2013 and its relative change over eight years. The relative biomass increments of *P. serotina* ranged from 0 to 22,000-fold. The success of *P. serotina*, expressed as aboveground biomass and biomass increment, varied among different tree species stands, but was greater under conifers. Total biomass of *P. serotina* depended on light and propagule availability while biomass increment depended on the change in tree stand biomass, a metric corresponding to tree stand maturation. Our study quantified the range of invasion intensity, expressed as biomass increment, in a forest common garden experiment with 14 tree species. Canopy cover was the most important variable to reduce susceptibility to invasion by *P. serotina*.

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Even a modest decrease of overstory biomass, e.g. caused by dieback of coniferous species, may be risky in areas with high propagule pressure from invasive tree species. Thus, *P. serotina* control may include maintaining high canopy closure and supporting natural regeneration of tree species with high leaf area index, which shade the understory.

Keywords
Allometric equations, biomass, invasion dynamics, light availability, natural regeneration, tree species effect

Introduction

Although invasive trees and shrubs are a worldwide problem (Richardson and Rejmánek 2011; Rejmánek and Richardson 2013), their impacts and mechanisms of ecological success are insufficiently understood. Their longevity and the long duration of their lag period (Kowarik 1995; Lonsdale 1999), as well as the physically large dimensions of invasive woody species, make research more challenging (Richardson and Rejmánek 2011). Invasive tree and shrub species are often classified as "transformers" (Richardson et al. 2000), due to the ability of these species to modify habitats. Invasive trees modify light conditions, usually decreasing light availability (Knight et al. 2008; Mueller et al. 2016) and increase rate of soil nutrient cycling (Binkley and Valentine 1991; Allison and Vitousek 2004; Reich et al. 2005). Due to this potential, invasive species of trees and shrubs are a serious threat to the environment (Richardson 1998; Richardson and Rejmánek 2011; Hawkins et al. 2015; Aerts et al. 2017). On the other hand, these properties of trees also highlight the potential role of native tree species in shaping ecosystem invasibility, by creating regeneration niches for invaders (Knight et al. 2008; Jagodziński et al. 2018) or closing them, by providing unfavorable conditions (e.g. González-Muñoz et al. 2014; Nyssen et al. 2016; Dyderski and Jagodziński 2018).

There are three crucial elements shaping invasion success: ecosystem invasibility, propagule pressure, and species invasiveness (Lonsdale 1999; Richardson et al. 2000). In the case of forest ecosystems, the level of resources (e.g. light, water, nutrients) is relatively constant compared to other ecosystems, due to the low frequency of disturbances within a single forest patch (Herben et al. 2016). Furthermore, differences in the availability of these resources across sites with similar soil and climate are determined mainly by tree species composition (see previous paragraph) and tree density (Jagodziński and Oleksyn 2009). However, disturbances in forests, regardless of their spatial scale, are usually connected with increased resource availability (Verheyen et al. 2003; Chmura and Sierka 2007). Although forest ecosystems usually return to a dynamic equilibrium state after disturbance (Gunderson 2000; Johnstone et al. 2016), the pulse of resource availability is crucial for success of invasive species (Davis et al. 2000). However, establishment of alien species also requires the presence of propagules, and the capacity of alien species to spread is crucial for determination of invasiveness (Richardson et al. 2000). The quantity of available propagules determines propagule pressure, which may be approximated by the number of mature plants (Vanhellemont et al. 2009) and the distance to the nearest

propagule source (Deckers et al. 2005; Pairon et al. 2006a; Jagodziński et al. 2015) or area of alien species cultivation (Pyšek et al. 2009).

Few studies of invasive trees and shrubs have quantified the density and size of different life stages during the initial stages of invasion. Because seedlings are more vulnerable to environmental conditions (e.g. drought, frosts or herbivory) than adult trees (Niinemets and Valladares 2006), their survival and recruitment into adult life phases is important for shaping future tree stand composition (Baraloto et al. 2005). Moreover, there is a lack of long-term studies which focus on the dynamics of species invasion and provide a quantitative assessment of the process.

Due to different invasion metrics used in fully controlled experiments and those used in field assessments, there is a gap in transferability of results between these two types of studies. Experiments in fully controlled conditions have measured invader success as relative growth rate or biomass (e.g. Grotkopp et al. 2010). In contrast, field studies usually measure alien species presence/absence, cover, or density (e.g. Pauchard et al. 2009; Jarošík et al. 2011; Kowarik et al. 2013; Woziwoda et al. 2014). Thus, field studies that quantify the invasive potential of alien species using the metrics of invasion success which are used in experiments, e.g. biomass, would provide discernment between findings due to ecological processes and those due to differences in measurement techniques. Biomass may provide a better measure of ecological success, reflecting space filled by the species, and is also a proxy of plant fitness (Younginger et al. 2017).

We took advantage of the invasion of *Prunus serotina* Ehrh. into an experimental forest common garden comprised of different tree species. The wide range of ecological characteristics of the cultivated species, similar soil parent material, climate and site history, and presence of alien species, compromise an ideal experimental design for invasion ecology studies (Knight et al. 2008; Jagodziński et al. 2018). The results would facilitate better recognition of the threats and management vulnerabilities of particular invaders.

Our study addresses the following questions: (1) how did invasion intensity, expressed as total biomass of *P. serotina*, change over eight years? and (2) how was this change connected with changes in light availability, tree stand maturation and seed source availability?

Methods

Studied species

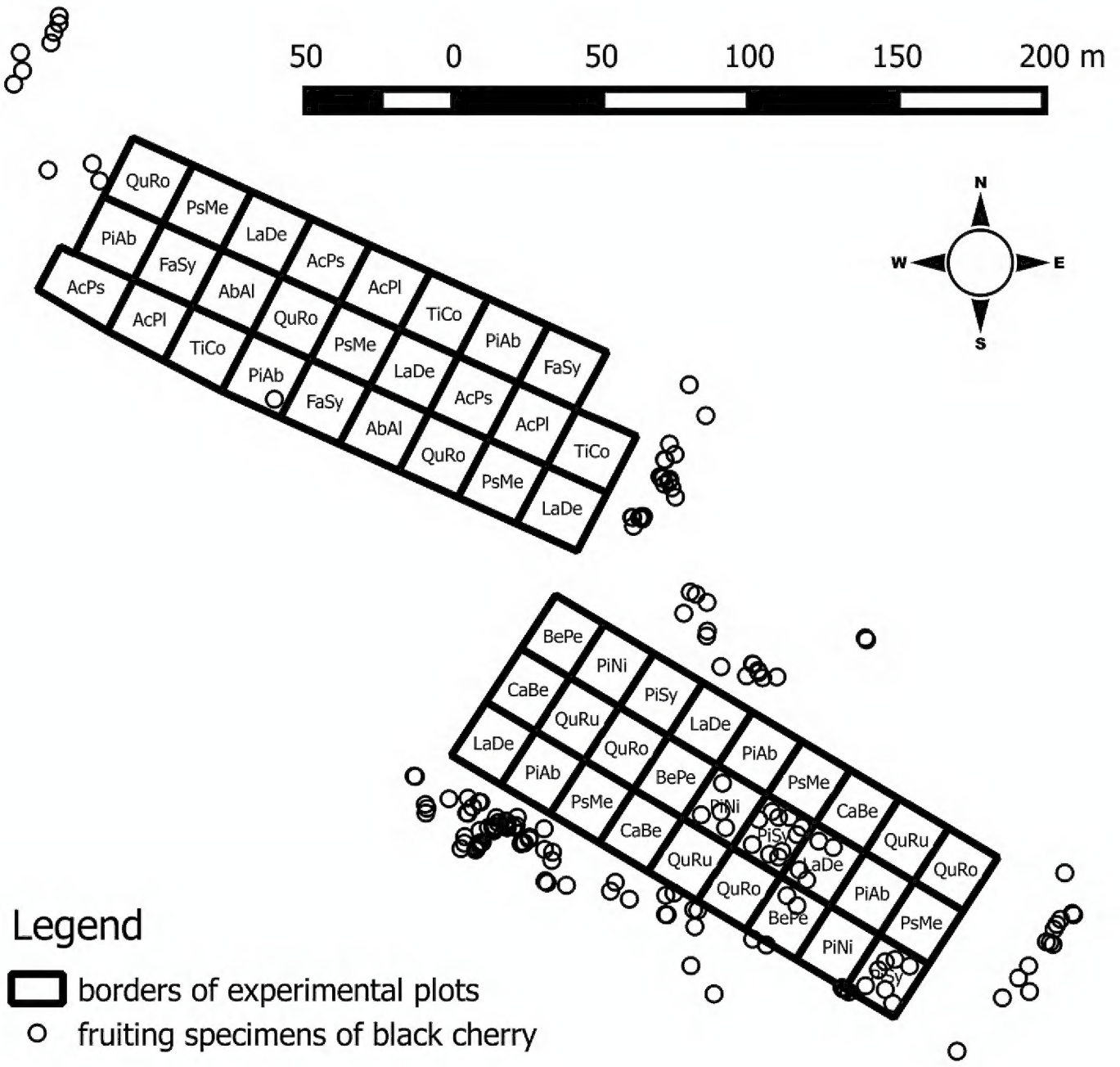
One of the most common invasive species of trees and shrubs in Europe is *P. serotina* (black cherry). It is a tree species from the Rosaceae family, with a natural range in the eastern part of North America, where it occurs in a wide range of habitats (Burns and Honkala 1990). Due to its high-quality timber and aesthetic values, *P. serotina* was introduced to Europe in the 17th century, first as an ornamental shrub in gardens, and then as a timber tree (Starfinger et al. 2003; Godefroid et al. 2005). In the 20th

century it was widely used as soil improver, due to its high-quality leaf litter (Starfinger et al. 2003; Godefroid et al. 2005; Horodecki and Jagodziński 2017; Horodecki et al. 2019). It has been reported in 22 European countries (Klotz 2007). This species limits growth of native species beneath its canopy (Robakowski and Bielinis 2011; Halarewicz and Żołnierz 2014; Aerts et al. 2017; Hamm et al. 2017). Due to the extent of its distribution, as well as the length and expense required for its eradication, in forest management in Belgium and the Netherlands *P. serotina* is treated as a target species in silviculture, due to its valuable timber (Starfinger et al. 2003; Nyssen et al. 2016). Black cherry seeds are transported by birds and mammals up to 600 m (Deckers et al. 2008; Jagodziński et al. 2015), however, densities of its seedlings are highest in the nearest neighborhood of maternal trees (Pairon et al. 2006b). It can start fruiting at ages of 7–10 years (in full light), while the peak of fruit production is at ages of 30–100 years (Burns and Honkala 1990; Starfinger et al. 2003).

Black cherry was most frequently introduced in intermediate-fertile habitats of mixed-coniferous sites, forests of poor site quality with *Quercus* spp., and in *Pinus sylvestris* stands where it occurs the most frequently (Godefroid et al. 2005; Zerbe and Wirth 2006). Because it has been planted mainly on less-fertile, sandy soils (Muys et al. 1992; Starfinger et al. 2003; Nyssen et al. 2016) *P. serotina* is less frequent on more fertile sites. However, within plantations of coniferous species on habitats of fertile deciduous forests, *P. serotina* can reach densities up to 25,660 ind. ha^{-1}, including 20,690 individuals up to 0.5 m tall (Jagodziński et al. 2015). One of the most important factors influencing invasion success of black cherry is light availability (Closset-Kopp et al. 2007; Chabrerie et al. 2008; Vanhellemont et al. 2009). Seedlings of *P. serotina* can grow slowly in unfavorable light conditions, waiting for overstory tree mortality and gap creation. This suggests that *P. serotina* may be a passenger rather than a driver of disturbance in forest ecosystems (Chabrerie et al. 2008).

Study area

The study was conducted in the Siemianice Experimental Forest in Poland (51°14.87'N, 18°06.35'E, elev. 180 m a.s.l.). The mean annual temperature is 8.2 °C, the mean annual precipitation is 579 mm and the growing season (considered as the number of days with mean temperature ≥ 5 °C) length is 213 days (Reich et al. 2005). The common garden experiment consists of 53 plots (0.04 ha each), with monocultures of 14 tree species: *Abies alba* Mill., *Acer platanoides* L., *A. pseudoplatanus* L., *Betula pendula* Roth., *Carpinus betulus* L., *Fagus sylvatica* L., *Larix decidua* Mill., *Picea abies* (L.) Karst., *Pinus nigra* Arn., *P. sylvestris* L., *Pseudotsuga menziesii* Franco, *Quercus robur* L., *Q. rubra* L., and *Tilia cordata* Mill. (Fig. 1). All species are native to the European temperate zone, except *P. nigra* (Mediterranean), *P. menziesii* (Pacific shore of USA) and *Q. rubra* (eastern USA). The plots were established in 1970 and 1971 and were arranged in two blocks, differing in initial soil fertility, which was modified after 30 years of different tree species cultivation (Szymański 1982; Reich et al. 2005). Nine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Legend
borders of experimental plots
fruiting specimens of black cherry

Figure 1. Distribution of experimental plots in Siemianice Experimental Forest and locations of fruiting specimens of *Prunus serotina* in 2013 in the nearest neighborhood of plots (up to 50 m). Labels are abbreviations using the first two letters of genus and species names, e.g. *Acer pseudoplatanus* = AcPs.

of the species were planted in three plots in one of the blocks (n = 3; Fig. 1), while *L. decidua*, *P. abies*, *P. menziesii*, and *Q. robur* were planted in three plots in each of the blocks (n = 6) and for *A. alba* one plot did not survive (n = 2; Reich et al. 2005; Knight et al. 2008). Seedlings used in the experiments were sown in the nursery in 1969 and planted in 1970/1971 with initial plant density of 10000 ind. ha^{-1} i.e. 399 plants per plot (19 rows × 21 plants at 1 m spacing; Reich et al. 2005). Within some plots there are small admixtures of pioneer tree species: *B. pendula*, *Populus tremula* L. and *Salix caprea* L. However their proportion of stand basal area is less than 5%. Trees on some study plots were damaged during windthrows in 2011, mainly those with *P. abies*.

Prunus serotina appeared within the experimental plots before 2005, as the tallest specimen measured in 2005 was 285 cm tall (Knight et al. 2008). Due to the ability of *P. serotina* to grow slowly under unfavorable conditions (Closset-Kopp et al. 2007), it is difficult to estimate when the first specimens appeared. As *P. serotina* reaches mean

annual height increments of 32.0 ± 8.9 cm (Closset-Kopp et al. 2007), the first individuals may have appeared in or before ca 1998, based on the height of the largest individual. In 2005, there were no fruiting *P. serotina* specimens in the nearest neighborhood (up to 50 m) of the experimental plots, but fruiting individuals were present up to 200 m from the site (Knight et al. 2008). We decided to use a threshold of 50 m as ca 80% of *P. serotina* fruits fall beneath canopy of parental trees (Pairon et al. 2006b) and density of *P. serotina* regeneration decreases strongly further than 50 m from the seed source (Jagodziński et al. 2015). For that reason, we considered propagule pressure in 2005 as constant for each study plot. In 2013, we found 132 fruiting specimens of *P. serotina*, but they were grouped mostly south and south-east of the experimental system (Fig. 1). Nevertheless, neither distance from the nearest fruiting *P. serotina* nor the number of fruiting trees within 50 m differed statistically significantly ($p > 0.05$) among plots with different tree species. For that reason, we treated proxies of propagule pressure measured in 2013 (distance from the nearest fruiting tree and the number of fruiting trees within a 50 m radius) as variables expressing the difference in propagule pressure between the two study dates.

Data collection

In 2005 and in September 2013, all specimens of *P. serotina* were investigated within all 53 experimental plots. We measured the root collar diameter (RCD) and height (H) of each tree and we determined its location within the plot with 0.25 m accuracy. Following Knight et al. (2008), we chose 1 mm RCD as a threshold to distinguish current-year from second-year or older specimens. The two size classes were distinguished due to low survival of seedlings after the first year (Dyderski and Jagodziński under review).

Biomass, as a function of both the dimensions and the density of plants, directly results from of invasive species growth, thus providing an approximation of invasion success. To assess the biomass of *P. serotina* within the experimental plots we harvested a subsample 59 trees (from a total population of 2339) for biomass estimation. We randomly selected 58 trees to harvest from the database of all measured trees, ordered by increasing RCD and H, plus the tallest tree, which was chosen to ensure coverage of the entire range of dimensions ($n = 59$; Suppl. material 2, Fig. S1). The selection was based on division of the dataset into equal intervals across increasing RCD and height. Then, we preselected trees with particular dimensions within particular study plots and in field we cut the first encountered tree with a given dimension. Model trees were harvested, oven-dried at 65 °C to constant mass and weighed with an accuracy of 0.001 g. Aboveground biomass (AB) of model trees ranged from 0.014 to 26546.52 g. Based on tree dimensions and masses, we developed allometric equations to estimate aboveground biomass (AB; [g]) of *P. serotina* within plots. For smaller trees (up to 10 mm RCD, $n = 52$) $AB = 0.3066 \cdot (RCD^2H)^{1.0165}$, with RMSE = 0.4 g and R^2 of the linearized model, i.e. transformed into $\ln(AB) = a + b \cdot \ln(RCD^2H)$ form, was 0.997.

For larger trees (10–126 mm RCD, $n = 7$) $AB = 0.3576 \cdot (RCD^2H)^{0.9445}$, with RMSE = 7.8 g and the R^2 of linearized model was 0.999. Models were chosen based on Akaike's Information Criterion (AIC; Suppl. material 2, Table S2). We applied these models to the results of the inventory from 2013 to obtain information about biomass in 2013.

To assess propagule pressure, we used a GPS receiver to map fruiting trees up to 50 m from each plot, as the probability of occurrence of *P. serotina* natural regeneration is highest within this distance (Jagodziński et al. 2015). We also recorded fruiting *P. serotina* within the study plots. This data allowed calculation of two proxies of propagule pressure: distance to the closest seed tree, which may be more important in cases of longer dispersal distances, and the number of fruiting trees within a 50 m radius (see rationale in study area description). We also investigated tree stand structure of the overstory, by measurements of diameter at breast height of all trees within the plots (Suppl. material 1, Table S1). For each plot, we calculated tree stand biomass using allometric equations specific to each species (Suppl. material 3, Table S3) in 2013 and in 2005. To quantify light availability, we measured the canopy openness index (diffuse non-interceptance; DIFN) each month during the growing season (June–August) of 2005 and 2013 using a LAI-2000 and LAI-2200 plant canopy analyzers (Li-Cor Inc., Lincoln, NE, USA) following the methods used in Knight et al. (2008). We took 20 measurements at six locations near the center of each plot at the height of 0.5 m above ground. DIFN indicates the fraction of open-field diffusive solar radiation reaching the forest floor.

Data analysis

We calculated relative increments of biomass for tree stands and for *P. serotina* as $(B_{2013}-B_{2005})/B_{2005}$, where B_{2005} – biomass in 2005 and B_{2013} – in 2013. We used relative increments to account for the effect of initial biomass from population dynamics within the study period. Tree stand biomass change was used as a proxy for tree stand maturation, describing increments of tree quantity in the ecosystem. In the case of negative values, biomass change may reflect quantity of trees destroyed during disturbances. Tree stand maturation is also connected with decrease of light availability (Hamm et al. 2017). Although biomass change mainly expressed tree stand productivity, in our case, when some tree stands were damaged, this variable expressed the quantity of damage (in cases of negative values of biomass). To analyze impacts of tree stand maturation (expressed as the change in tree stand biomass), light availability (DIFN) and propagule pressure (distance to the nearest fruiting tree and number of fruiting trees up to 50 m) on biomass crop and biomass relative change of *P. serotina* we used generalized additive mixed models (GAMM), describing the additive interactions between the analyzed predictors. As mixed-effects models, GAMM also allowed us to handle study design by including random effects describing study block (Fig. 1). GAMMs were prepared using the *mgcv* package (Wood 2011). We compared GAMMs using Akaike's Information Criterion to choose the best fit model. Differences between tree stands

in *P. serotina* biomasses and densities were tested using Kruskal-Wallis tests, due to the small number of samples and lack of normality. All analyses were conducted in R software (R Core Team 2017).

Results

Changes of *P. serotina* density within experimental plots

Within the 53 experimental plots, the number of *P. serotina* specimens increased from 556 in 2005 to 2339 in 2013. Density of *P. serotina* in experimental plots in 2013 ranged from 0 ind. ha^{-1} (in a plot with *A. alba* and a plot with *Q. rubra*) to 7895 and 8471 ind. ha^{-1} in plots with *P. abies* (Suppl. material 4, Table S4). Overall density of *P. serotina* populations increased statistically significantly in plots with *L. decidua*, *P. abies*, *P. menziesii*, and *Q. robur* (Fig. 2). The differences were from double (*L. decidua*) to almost 23-fold (*P. abies*). For seedlings < 1 mm RCD, the difference between 2005 and 2013 inventories was significant only beneath *P. menziesii*, and for older trees (with RCD > 1 mm), differences in density were statistically significant in plots with *L. decidua*, *P. menziesii* (5-fold), and *Q. robur*. The differences between the two study dates in mean overall density were statistically significant for all coniferous species grouped together (315.2 ± 87.5 in 2005 and 1668.6 ± 438.7 in 2013; $p < 0.001$) and all deciduous species grouped together (216.9 ± 48.2 in 2005 and 565.2 ± 179.8 in 2013; < 0.05).

Changes in experimental tree stands and propagule availability

During the study period, almost all tree stands increased their biomass, with the exception of *P. abies* stands (–13.9 ± 4.7 Mg ha^{-1}), where mortality exceeded growth (Suppl. material 4, Fig. S2a–c). Growth dynamics were species dependent ($p < 0.001$) – the highest biomass increment was in stands of *Q. rubra* (85.0 ± 14.8 Mg ha^{-1}), *A. pseudoplatanus* (81.4 ± 14.7 Mg ha^{-1}), *F. sylvatica* (80.4 ± 9.4 Mg ha^{-1}), and *P. menziesii* (71.2 ± 3.3 Mg ha^{-1}), and the lowest in *C. betulus* (7.7 ± 2.2 Mg ha^{-1}). Nevertheless, the highest biomass increment was found in plots near the experiment's border located near the paths. Tree growth caused decreased light availability in 39 of 53 plots, although light availability increased in *P. abies* and *P. menziesii* tree stands (Suppl. material 4, Fig. S2d–f). Change in light availability differed among tree species ($p < 0.001$): the largest increases were in stands of *P. abies* (0.038 ± 0.007) and *P. menziesii* (0.010 ± 0.005), and the largest decreases were in stands of *P. nigra* (–0.070 ± 0.019), *Q. robur* (–0.071 ± 0.008), *P. sylvestris* (–0.080 ± 0.028), *L. decidua* (–0.103 ± 0.019) and *B. pendula* (–0.110 ± 0.017). In 2005 there were no fruiting *P. serotina* specimens within 50 m of the plots, but some were present up to 200 m away (Knight et al. 2008). In 2013, only six plots were farther than 50 m from the nearest fruiting *P. serotina* and most of the plots were located near at least five fruiting trees (Suppl. material 4, Fig. S3).

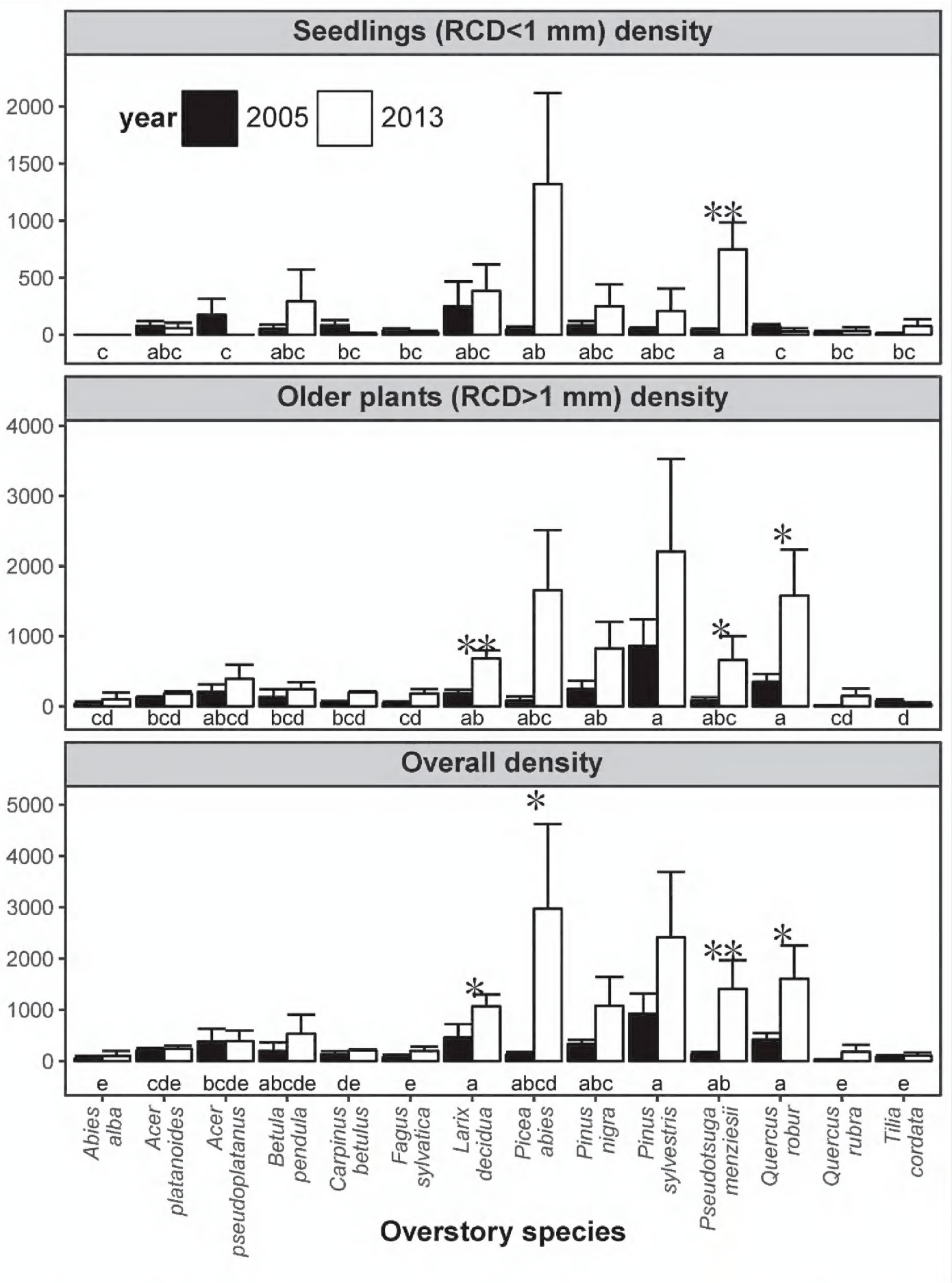

Figure 2. Mean +SE density (ind. ha^{-1}) of *Prunus serotina* within experimental plots of 14 tree species in 2005 and in 2013. Asterisks mark significance levels of differences between inventories in 2005 and 2013 (* – $p < 0.05$, ** – $p < 0.01$), based on Student's t-test. Letters under bars represent significance of differences among tree species in 2013, based on Kruskal-Wallis tests; there are no statistically significant differences between values marked by the same letter.

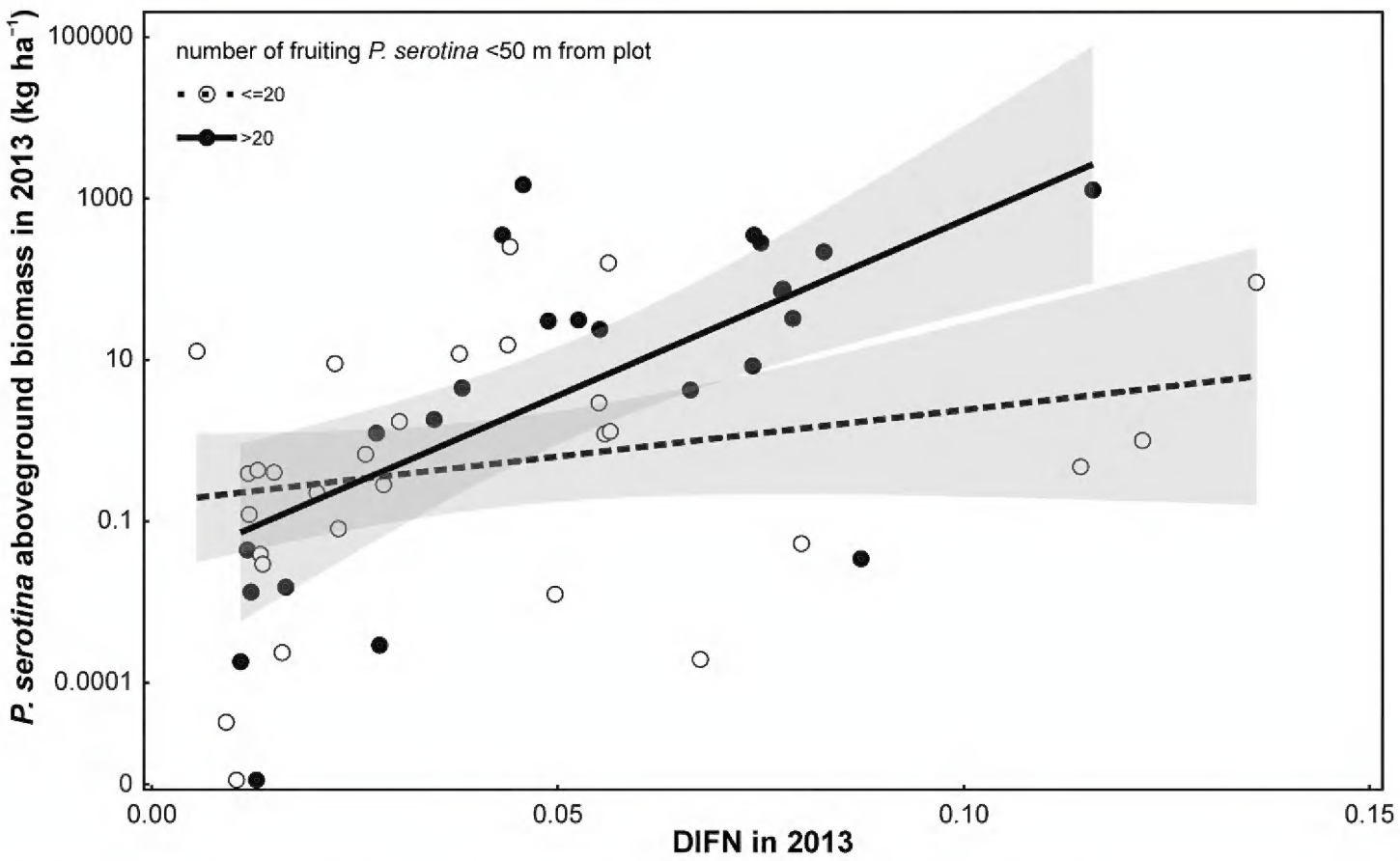

Figure 3. Relationship between light availability, expressed by DIFN, and aboveground biomass of *P. serotina*, in two classes of propagule pressure, expressed by the number of fruiting *P. serotina* trees up to 50 m from the plot (open dots and dashed line :≤ 20; solid dots and line: > 20; $p < 0.001$, $R^2 = 0.32$). Threshold of 20 trees was chosen according to median and mean for all plots (18 and 18.49, respectively). Modification given by class of propagule pressure was statistically significant ($p < 0.01$). Note log-transformation of the y axis. Shading around regression lines indicate range of model SE.

Aboveground biomass of *P. serotina*

Biomass of *P. serotina* increased in almost all plots (except six; Suppl. material 4, Fig. S3). In 2005 total biomass varied from 0 to 144.4 kg ha^{-1} (*P. sylvestris*) and in 2013 from 0 to 1485.6 kg ha^{-1} (*P. sylvestris*). Biomass in 2013 differed among tree species stands ($p < 0.01$): the highest was in *P. sylvestris* (922.0 ± 464.0 kg ha^{-1}), *P. nigra* (143.00 ± 107.3 kg ha^{-1}), and *L. decidua* (112.6 ± 66.0 kg ha^{-1}), and the lowest in *T. cordata* (0.005 ± 0.004 kg ha^{-1}) and *Q. rubra* (0.006 ± 0.005 kg ha^{-1}). Relative increment of *P. serotina* biomass differed among tree stand species ($p < 0.01$): the highest values occurred in stands of *P. abies* (742,453.1 ± 390,415.3%), *F. sylvatica* (155,700.5 ± 93,531.8%), and *B. pendula* (129,014.4 ± 125,740.1%), and the lowest occurred in *Q. rubra* (1,150.5 ± 668.4%), *A. platanoides* (570.1 ± 309.8%), *A. alba* (306.1 ± 306.1%), and *T. cordata* (–39.3 ± 39.3%). Analysis of the factors responsible for invasion success has shown that total biomass of *P. serotina* in 2013 depended on propagule pressure (number of fruiting *P. serotina* up to 50 m and minimal distance to fruiting *P. serotina*) as well as light availability ($R^2 = 0.696$; Table 1, Figs 3, 4). Relative increment of *P. serotina* biomass depended on the change in tree stand biomass ($R^2 = 0.415$; Fig. 4).

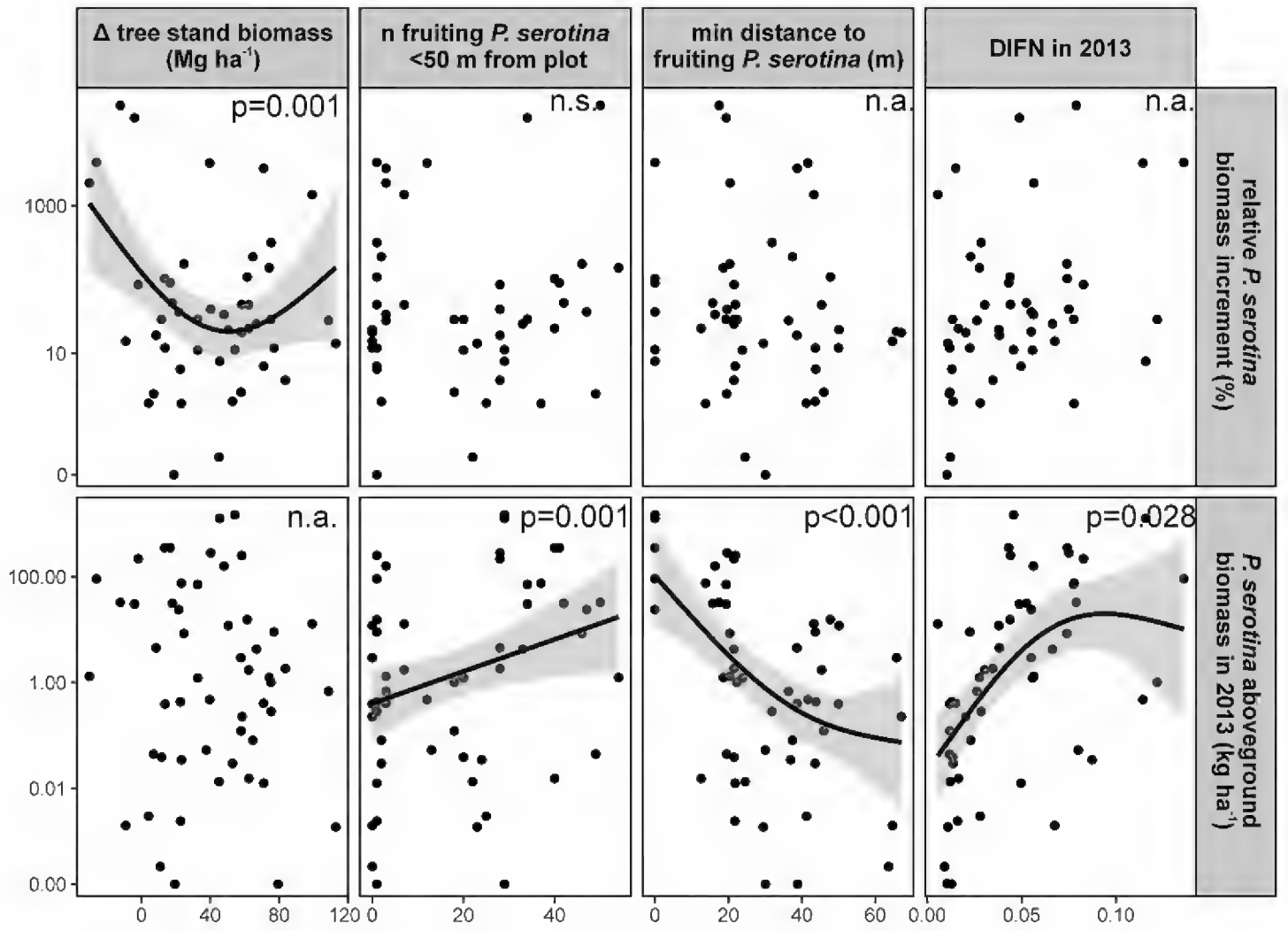

Figure 4. Responses of percentage increment of *Prunus serotina* biomass and total biomass in 2013 to the particular predictors. Lines were fitted using General Additive Models (see Table 1 for model parameters), grey area indicates SE of model, n.s. – not significant, n.a. – significance level not applicable as considered variable was not included in the final model (Table 1). Note the logarithmic scale of the Y axis.

Table 1. General Additive Models describing predictors of percentage increment of *Prunus serotina* biomass and total biomass in 2013. The best model was chosen according to AIC. AIC of null model refers to model with an intercept only, to express a final model inertia; edf – estimated degree of freedom, Ref. df – reference degree of freedom, used for F test for *p*-value computation

Estimated variable	**Percentage increment of *P. serotina* biomass**				**Biomass of *P. serotina* in 2013**			
Parametric coefficients:	**Estimate**	**SE**	**t**	**p**	**Estimate**	**SE**	**t**	**p**
(Intercept)	1032.700	401.300	2.573	0.014	91.070	20.720	4.396	<0.001
Approximate significance of smooth terms:	**edf**	**Ref.df**	**F**	**p**	**edf**	**Ref.df**	**F**	**p**
change of tree stand biomass	3.456	4.282	3.316	0.001	–	–	–	–
number of fruiting *P. serotina* up to 50 m	1.095	1.182	3.134	0.090	5.191	6.249	4.608	0.001
min distance to fruiting *P. serotina*	–	–	–	–	3.426	4.064	15.952	<0.001
DIFN in 2013	–	–	–	–	5.469	6.520	2.633	0.028
random effect (block)	<0.001	1.000	0.000	0.659	<0.001	1.000	0.000	0.768
Model parameters	**R^2**	**Deviance explained**	**AIC**	**AIC of null model**	**R^2**	**Deviance explained**	**AIC**	**AIC of null model**
	0.254	31.9%	1018.2	1027.7	0.696	77.9%	700.9	748.2

Discussion

We found the highest intensities of invasion, expressed as relative biomass change, within plots with low *P. serotina* density in 2005. In these plots, invasion accelerated later, which was indicated by the high proportion of seedlings compared to older plants (Fig. 2). In both 2005 and 2013, we found higher densities of older *P. serotina* in plots invaded earlier, where biomass of *P. serotina* was the highest. In both 2005 and 2013 the highest total biomass was in plots with *P. sylvestris*. Within these plots the presence of older trees, with higher height and diameter increments, could have decreased light availability, causing decreased seedling survival (Knight et al. 2008; Dyderski and Jagodziński under review) or lengthened persistence in a "seedling" stage (Mulligan and Munro 1981; Closset-Kopp et al. 2007). Beneath *P. sylvestris*, most *P. serotina* biomass was concentrated in old, often fruiting individuals, responsible for high densities of seedlings, connected with high propagule pressure. However, due to poor seedling recruitment to the shrub layer, the density of older plants was low, similar to the mechanism described by Godefroid et al. (2005). A similar pattern was observed in the plots with *B. pendula*, *L. decidua*, and *P. nigra*. Our study also suggests that disturbance, which led to decreases of tree stand biomass and canopy closure on some plots, acted as a pulse of increased light availability. This window of opportunity allowed rapid *P. serotina* invasion, consistent with the Fluctuating Resource Availability Theory of Invasibility (Davis et al. 2000). However, the relationship between biomass of *P. serotina* and light availability was strongly modified by propagule pressure (Fig. 3). The compound effect of propagule pressure and invasibility is known from earlier conceptual studies (Davies et al. 2005). Our other field study (Dyderski and Jagodziński 2018) also confirmed the superior role of propagule pressure over invasibility.

The species-dependent pattern of invasion success resulted from different life history traits of particular species. One of them is growth dynamics, shown by differences in biomass and biomass increment of overstory trees. At the same age, some of them may exhibit different growth stages, due to different costs of growth, connected with specific stem density (Díaz et al. 2016). Moreover, tree species create different light availability due to different branching architecture and foliage morphology (Breuer et al. 2003; Knight et al. 2008; Pretzsch 2009). Earlier invasion was found in the stands of pioneer tree species, where canopy closure and reopening due to self-thinning occurred earlier (Szymański 1982; Jagodziński and Kałucka 2008; Pretzsch 2009). This pattern is consistent with observations that forests dominated by pioneer species are more invasible (Zerbe and Wirth 2006) or that late-successional tree species limit *P. serotina* invasion (Godefroid et al. 2005; Chabrerie et al. 2008; Jagodziński et al. 2015). Starfinger et al. (2003) claim that presence of dense thickets of *P. serotina* in *P. sylvestris* forests results from planting it as a soil improver in these poor habitats. In our study *P. serotina* spontaneously colonized experimental plots, without being intentionally planted. This indicates that although introductions increase initial propagule pressure, intentional introduction into poor habitat was not crucial for invasion success of *P. serotina* in the study site.

Higher total biomass and increment of *P. serotina* in stands of coniferous species may also result from habitat modification by these species, i.e. higher nutrient leaching and acidification (Binkley and Valentine 1991). This effect of tree species is independent of modifying light availability. In our plots coniferous species had lower soil and litter pH, lower calcium content, and higher acidity, which resulted from different elemental contents of foliage (Reich et al. 2005; Mueller et al. 2012). These factors decrease abundance of understory vegetation (Chmura 2013), which competes with naturally established regeneration of invasive species (Knight et al. 2008; Jagodziński et al. 2018). Thus, coniferous tree stands, especially when planted on fertile sites, are more invasible due to negative tree species effects on understory vegetation cover (Zerbe and Wirth 2006; Jagodziński et al. 2015).

Studies on populations of *P. serotina* reveal that the proportion of seedlings and specimens in the herb layer (< 50 cm height) is very high. In Rogów Arboretum, within a sample of 20,843 specimens, 76.7% of them were < 50 cm height (Jagodziński et al. 2015). In Compiègne forest, seedlings comprised 72.1% of a sample of 4994 specimens (Closset-Kopp et al. 2007). As presence of *P. serotina* in the shrub layer limits development of the herb layer (Godefroid et al. 2005; Halarewicz and Żołnierz 2014, but see Chabrerie et al. 2008), it also limits the growth of its own offspring. Therefore, we may observe either low or high densities of young *P. serotina* under tree stands where the species fruits. However, in both scenarios *P. serotina* biomass is low. The high density of seedlings and low biomass of *P. serotina* is connected with shade intolerance of older *P. serotina* specimens (Burns and Honkala 1990). Therefore, mere consideration of density does not reflect invasion dynamics unless seedlings and older trees are considered separately. In contrast, biomass is a function of both density and dimensions of plants, and thus, it increases with increase of both parameters. For that reason, biomass assessment may yield a more accurate understanding of invasion dynamics than density alone.

Our study confirmed the sit-and-wait strategy of *P. serotina* (Closset-Kopp et al. 2007) over a longer time interval by showing the potential for quick increase of biomass after rapid increase of light availability caused by the windthrow. Persistence of the seedling bank and waiting for the window of opportunity allows this species to colonize forest ecosystems which are usually less invasible due to the low frequency of disturbances (Herben et al. 2016). Our study confirms observations of Chabrerie et al. (2008), who found *P. serotina* as a passenger rather than a driver of disturbances. A similar pattern of emergence after dieback of the overstory trees was observed for *Sorbus aucuparia* in mountain *P. abies* forests (Żywiec et al. 2013). *P. serotina* in its native range is a species able to dominate secondary succession after disturbances caused by windthrow, logging, or fire (Mulligan and Munro 1981).

Similar to Vanhellemont et al. (2009), we found that colonization of uninvaded areas is a combined effect of long-distance dispersal events in combination with windows of opportunity. However, our study had more emphasis on the role of propagule pressure, which is expressed by distance to the seed source and number of fruiting trees. The roles of the distance from the propagule source and invader density, modified by

type of tree stand, was confirmed in our previous study (Jagodziński et al. 2015). Long-distance dispersal, mostly bird-mediated (Deckers et al. 2008; Dylewski et al. 2017), comprises only 20% of seeds and the remaining 80% fall in the vicinity of parent trees (Pairon et al. 2006b). This high input of seeds in the invaded sites is responsible for persistence of the seedling bank every year. The subset of bird-mediated seeds is responsible for colonizing new sites, and in the broader perspective it is responsible for expansion of the invaded range. Propagule pressure is one of the most relevant factors driving invasion potential of alien woody species in Europe (Pyšek et al. 2009), and similar to Vanhellemont et al. (2009), we found that low levels of it limit invasiveness of *P. serotina*, even in invasible plots (Fig. 3).

Our study, for the first time, quantified the range of an invader's intensity, expressed as biomass increment, in a forest common garden experiment with 14 tree species. Relative biomass increments of *P. serotina* ranged from 0 to 22,000-fold in eight years. This highlights the urgent need for monitoring even small populations of *P. serotina*, as this species has the ability for sudden outbreaks. Noticing even small but stable populations of *P. serotina* that have not reached the dimensions allowing reproduction will provide time for local eradication, which can lower the high cost of *P. serotina* control (Reinhardt et al. 2003).

Our results also recommend prioritized risk assessment for *P. serotina*, as was stated by Carboneras et al. (2018). Success of *P. serotina* varied among different tree species. Total biomass depended on light and propagule availability, while biomass increment depended on disturbances, described by changes in tree stand biomass. Invasion intensity was driven by disturbance, i.e. dieback of trees, especially *P. abies*, caused increases in light availability, which increased invasibility of these stands. In conjunction with propagule pressure, disturbance allowed growth and survival of numerous *P. serotina* seedlings. Our findings suggest that propagule pressure and disturbance intensity, expressed in biomass change, should be considered together to understand the susceptibility of forest stands to invasion and to develop methods of control for invasive trees and shrubs (Brundu and Richardson 2016). Even modest disturbances, including vulnerability to dieback in succession of coniferous species, may be risky in areas with high propagule pressure from invasive trees. Thus, silvicultural methods for *P. serotina* control may include maintaining high canopy closure and supporting natural regeneration of tree species with high leaf area, which shade the understory. This result is consistent with recommendations of Nyssen et al. (2016), who highlighted the importance of life history traits of the invaded species habitats in shaping invasibility.

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Supplementary material 1

Parameters of tree stands on experimental plots in the Siemianice Experimental Forest

Authors: Andrzej M. Jagodziński, Marcin K. Dyderski, Paweł Horodecki, Kathleen S. Knight, Katarzyna Rawlik, Janusz Szmyt

Data type: measurement

Explanation note: **Table S1.** Parameters of tree stands on experimental plots in the Siemianice Experimental Forest.

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Link: https://doi.org/10.3897/neobiota.46.30413.suppl1

Supplementary material 2

Procedure for modelling the allometric relationships between *P. serotina* dimensions and biomass

Authors: Andrzej M. Jagodziński, Marcin K. Dyderski, Paweł Horodecki, Kathleen S. Knight, Katarzyna Rawlik, Janusz Szmyt

Data type: measurement

Explanation note: **Table S2.** Summary of models of *P. serotina* biomass. Parameters of the best model were bolded. **Figure S1.** Distribution of sampled trees compared with root collar diameter and height of all investigated trees.

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Supplementary material 3

Allometric equations determining aboveground biomass of particular tree species presented on sample plots

Authors: Andrzej M. Jagodziński, Marcin K. Dyderski, Paweł Horodecki, Kathleen S. Knight, Katarzyna Rawlik, Janusz Szmyt

Data type: measurement

Explanation note: **Table S3.** Allometric equations determining aboveground biomass of particular tree species presented on sample plots. Equations adopted were established for habitat conditions similar to those of this study. Abbreviations: DBH – diameter at breast height; NA – not available.

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Supplementary material 4

Changes of *P. serotina* density, biomass and environmental parameters included in models

Authors: Andrzej M. Jagodziński, Marcin K. Dyderski, Paweł Horodecki, Kathleen S. Knight, Katarzyna Rawlik, Janusz Szmyt

Data type: measurement

Explanation note: **Table S4.** Changes of *P. serotina* leaf area index, density, biomass and environmental parameters included in models. Abbreviations: Δ – difference 2013-2005; %Δ – percent difference (2013-2005)/2005; LAI – leaf area index; DIFN – diffusive non—interceptance (flight availability expressed as a fraction of the open sky). **Figure S2.** Aboveground biomass of planted tree species [Mg ha-1] within tree stands: (a) – in 2005; (b) – in 2013; (c) – difference between 2013 and 2005; and light availability level – DIFN: (d) – in 2005; (e) – in 2013; (f) – difference between 2013 and 2005; **Figure S3.** aboveground biomass of *P. serotina* [kg ha-1]: (g) – in 2005 (h) – in 2013, (i) – difference between 2013 and 2005 and propagule pressure around the experimental plots: (j) – minimal distance from fruiting specimens [m] and (k) – number of fruiting *P. serotina* trees up to 50 m from the plot. Black dots in (j) and (k) indicate fruiting specimens of *P. serotina*.

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